The coexistence problem revisited

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New theoretical study warns against common misinterpretation of classical ideas on the limits to species diversity.

The great limnologist George Evelyn Hutchinson famously asked the question "why are there so many kinds of animals?"[1]. Hutchinson's answer to his own question has become one of the foundational ideas in ecology, and has to do with the abundance of "regulating factors" in the environment. However, the idea's deceptive simplicity can lead to important misinterpretations, as reported by Ashby et al.[2] in the current issue of *Nature Ecology & Evolution*.

Building on a classical theoretical model in which species possess a suite of traits and the degree of competition between them is governed by trait similarity, they show that the way competition should vary with trait distance depends sensitively on whether the different traits introduce new ways of being regulated. If not—and the authors argue that this case is typical—then the number of trait combinations which can coexist is much smaller than the full set of available ones, leaving many potential ecological possibilities unfilled.

Every species is a mind-boggingly complex solution to a unique evolutionary problem. But the confusing fact that there are more than eight million eukaryotic species alone[3] reveals an apparent contradiction in our ideas on how such diversity could arise in the first place. *If* we take it for granted that inferior types are discarded via natural selection, *then* why are there multiple species to begin with, instead of just the "best" one?

Darwin himself had struggled with this problem[4] and came to the realization[5] that species coexist when their populations do not grow at the others' expense. Let us take, for example, two bird species competing for use of the same nest sites. The success of one species at acquiring those sites then means there will be fewer left for the other, and so whichever species is better at acquiring the sites will drive the other extinct. However, if the species compete for different things—if they use different nest sites, for example—then the success of one species does not come at the expense of the other. Limitation by different factors keeping population growth in check (known as "regulating factors" by ecologists[6]) is thus the basis for species coexistence. While there are technical corrections to the rule that the number of species cannot exceed the number of regulating factors[7,8], it is still an important and general principle limiting species diversity.

Imagine that there are seeds of three different sizes (small, medium, and large, say) that bird species consume. This makes for three separate regulating factors and therefore at most three coexisting species. But now suppose that each of the seeds comes in three different shades: dull, normal, and shiny. We now have $3 \times 3 = 9$ distinct regulating factors: small dull seeds, medium dull seeds, and so on. The potential number of species has just increased from three to nine (Figure 1A). Now also imagine that the habitat in which the birds live is structured so that there are high, medium, and low altitude sites—in the same vein, we now have $3 \times 3 \times 3 = 27$ distinct resources. And so on: the number of distinct regulating factors (and therefore the number of potentially coexisting species) increases exponentially with every added independent property.

Knowing how complex natural environments can be, one might even think that eight million species[3] is a woefully small number compared to what could in principle be possible.

However, as pointed out by Ashby et al.[2], there is one kind of logical slip that is all too easy to make. Suppose there are small, medium, and large seeds, and also three different types of nest sites, say at high, medium, and low altitudes. How many species can persist? The correct answer is six, because that is the total number of independent regulating factors: three types of seeds, plus three types of nest sites. However, a naive analogy with our example above suggests that the answer is nine, because that is the number of distinct combinations of food sizes and nest site types (small seeds and low sites, medium seeds and low sites, and so on). But these combinations do not stand for distinct regulating factors: they represent various *pairings* of only six different factors (Figure 1B). Of course, one species may be adapted to eating large seeds and using low nest sites, while another to eating large seeds and using high nest sites. But even though these species have distinct habitats, they still compete over the same food and so are not regulated by independent factors. As Ashby et al.[2] put it, such combinations "open up new avenues of competition rather than providing species with alternative resources". That is, out of nine possible adaptive strategies, only a subset of at most six can actually be realized.

The contribution of Ashby et al.[2] warns against this misunderstanding in a remarkably clearly written piece. To be fair, they have reached their conclusions in a somewhat roundabout way. Instead of simply tallying the regulating factors (as we have done here), they initially proceed as if the right side of Figure 1B did actually represent nine separate factors, but then go on to give a mathematical recipe for calculating competition which effectively merges them into six again. Furthermore, it is unclear how their recipe could be generalized beyond the confines of the particular model they analyze. Despite this, the authors' main message that the number of coexisting species may be much lower than the number of distinct ecological possibilities still comes through loud and clear. If, after reading their article, people will wonder how ecologists could possibly have ever been confused by something that obvious, then it will have served its purpose.

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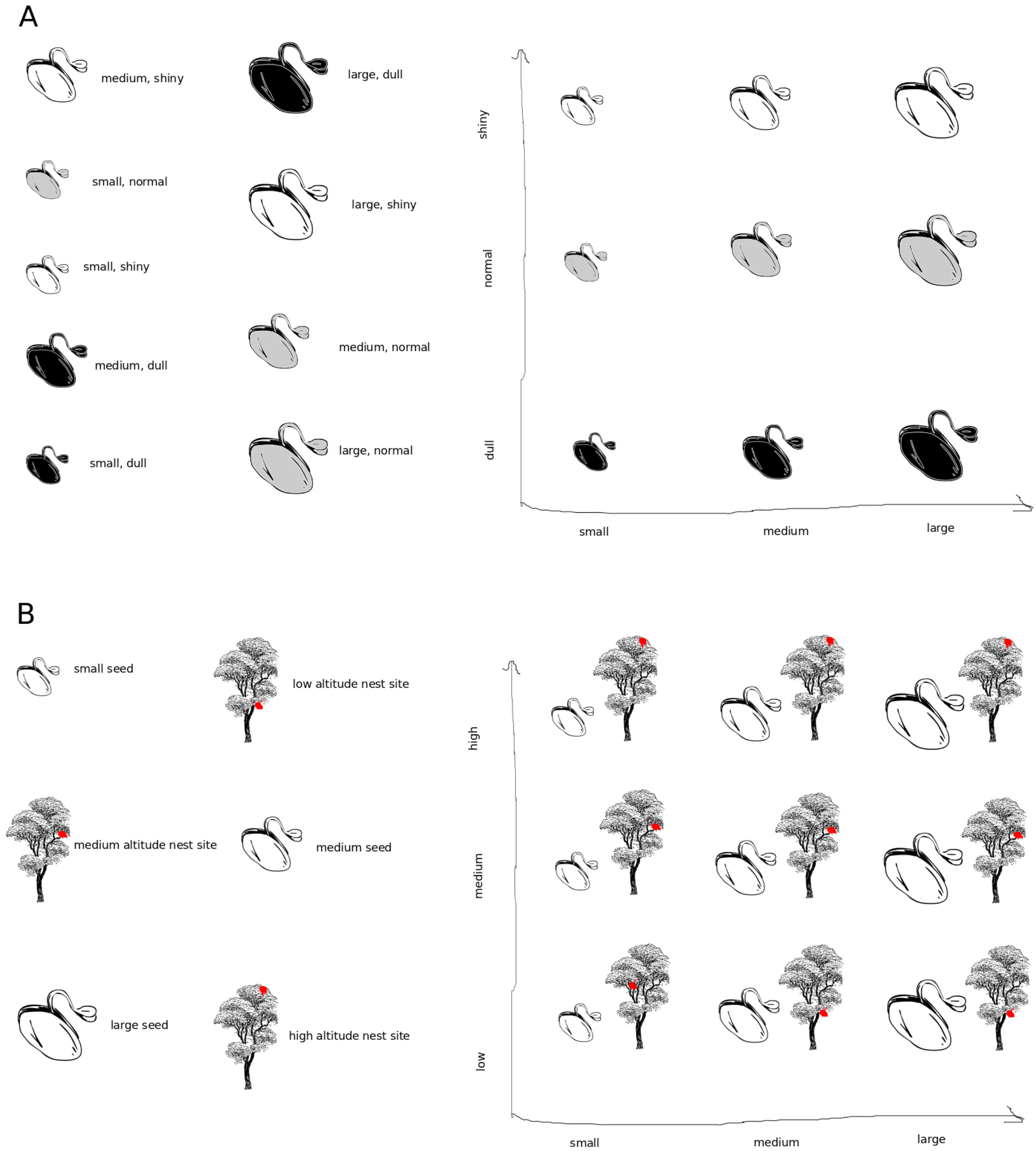

Figure 1: **A**: seeds come in three sizes and three colours. Thus, there are nine distinct types of seeds which can act as regulating factors. They can simply be listed as in a catalogue (left) in arbitrary order—including the neat arrangement along the two independent axes corresponding to size and colour (right). While this arrangement says nothing new, it may be easier to interpret for the human eye than the one on the left. **B**: there are three different types of seeds (small, medium, large), and also three types of nest sites (high, medium, and low altitude). The total number of regulating factors is six, as is obvious when making a catalogue list of them (left). However, there can be a temptation to visualize this scenario along two dimensions as before, with the axes corresponding to seed size and nest height (right). The points in this plane, however do not correspond to individual regulating factors. Instead, they correspond to various pairings of the six factors on the left—a conceptually completely different object that should not be confused with the one on the right of **A**.